

# THE EFFECT OF LEAF AGE ON THE PERFORMANCE OF THE BIRCH APHID *EUCERAPHIS BETULAE* (KOCH)

GARETH EDWARDS-JONES

*Edinburgh School of Agriculture, 42 South Oswald Road, Edinburgh EH9 2HH.*

## INTRODUCTION

Seasonal changes in the abundance of tree feeding aphids are well known (Dixon, 1969; Wratten, 1974). Abundance typically peaks in spring, decreases in midsummer and often rises again in the autumn. These patterns are probably caused by an interaction of seasonal variation in the suitability of leaves as a food source and density-dependent population processes such as wing production and/or migration (Dixon, 1971). Although changes in leaf water content, leaf toughness and chemical defence concentration are well known (Feeny, 1970; Ayres & Maclean, 1987), it is the concentration of soluble nitrogen in the leaves which is believed to be the most important factor in determining patterns of abundance in aphids (Mittler, 1958; Dixon, 1963, 1966, 1969). The autumnal increase in aphid reproductives which accompanies the mobilization of nutrients in senescent leaves, supports this view.

*Euceraphis* is a large and active aphid, with all generations being alate (possessing wings). The first (fundatrix) generation hatches from eggs in early spring, and gives rise to a series of parthenogenetically reproducing generations during the summer. The sexual generation (oviparae) are produced in the autumn, these mate and lay their eggs, usually around the base of buds and along adjacent twigs (Edwards-Jones unpublished observation). There are two British species in this genus; *Euceraphis betulae* (Koch), which is primarily associated with *Betula pendula* Roth, and *E. punctipennis* (Zett.) which is associated with *B. pubescens* Ehrh (Blackman, 1977).

This paper examines the effect of leaf age on the development and fecundity of the birch aphid *Euceraphis betulae*.

## MATERIALS AND METHODS

Six saplings of *Betula pendula* Roth (approx. 1 m high) were planted into pots in early January. Three saplings were chosen at random at the beginning of February and were placed in a greenhouse at 20 °C with a 16-h day-length in order to induce early bud-burst, and three were left outside in order to allow bud-burst at the normal time. On 2.iv.87 when the treatment saplings in the greenhouse had fully expanded leaves and the buds of the control group were close to bursting, all six saplings were moved into a constant temperature room at 10 °C, 70% relative humidity and a 16-h day-length. The saplings were watered regularly and mist sprayed daily with distilled water for the duration of the experiment.

Leaves were removed from each tree every 14 days between 21.iv.87 and 18.vi.87. These were analysed for toughness and soluble nitrogen content. Toughness was measured using a push-pull fruit tester, which estimated the force needed to push a circular metal rod of 5 mm diameter through the leaf lamina. Soluble nitrogen was measured by standard Kjeldhar method (van Emden & Bashford, 1969).

Eggs of *Euceraphis* were collected in Silwood Park, Ascot during the last week of March 1987, and were kept in a refrigerator at 5 °C until the beginning of the experiment. On 13.iv.87, by which time most *B. pendula* in the field had infestations of *Euceraphis*, the eggs were removed from the refrigerator and left at room temperature for 24 h. During this time the majority of eggs hatched. The newly hatched nymphs were introduced on to the saplings on 14.iv.87. Ten nymphs were placed on

each sapling. Nymphs were placed individually onto terminal buds or leaves. Muslin bags large enough to cover a single leaf, and secured around the supporting twig were used to contain the aphids.

Aphids were observed every other day, and the number of offspring produced per time interval was recorded. All second-generation nymphs were removed from their parent, and 56 were randomly allotted to one of the treatments and placed onto the relevant saplings as part of the second-generation experiment. As no nymphs were produced by individuals feeding on the mature leaves, only nymphs produced on the young buds were utilized in the second-generation experiment. Second-generation aphids were monitored in a similar fashion to those of the first generation. All third-generation nymphs were removed from the saplings, but not utilized in any further experiments. The experiment terminated on 20.vi.87 with the death of the last second-generation aphid.

### RESULTS

The level of soluble nitrogen was greater in young leaves than old on every sampling date (Fig. 1a). Leaf toughness increased throughout the experiment in both treatments (Fig. 1b), and was greater in old leaves than young on all dates prior to 18.vi.87, when the two measurements converged.

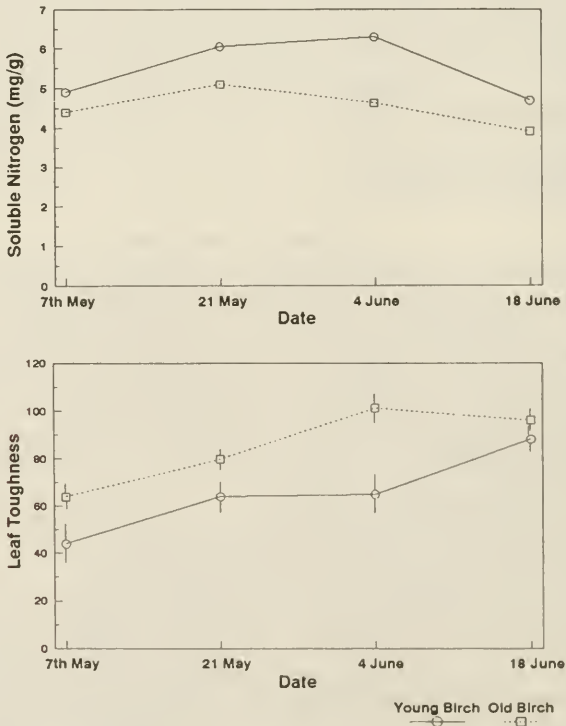


Fig. 1. Changes in the attributes of young and mature leaves of *Betula pendula*, (a) mean soluble nitrogen content and (b) leaf toughness. Bars are standard errors.

The differences in leaf quality between treatments were reflected in the aphid's performance (Table 1). No first-generation nymphs survived to adulthood on the mature leaves, and only two second generation nymphs reached maturity. The survival of nymphs was significantly greater on young leaves where approximately 50% of individuals reached maturity (two by two contingency table; generation 1, Yates' corrected  $\chi^2 = 10.5$ ,  $P < 0.01$ ; generation 2, Yates' corrected  $\chi^2 = 6.48$ ,  $P < 0.05$ ). The development time of individuals on old leaves was also longer than those on young foliage, and the average fecundity was lower.

Table 1. Survival, development and fecundity of first and second generation *Euceraphis betulae* on young and mature foliage of *Betula pendula*. Figures in parentheses are standard errors.

Generation:	Young leaves		Old leaves	
	1st	2nd	1st	2nd
Initial population size	30	26	30	30
Proportion alive after 7 days	0.77	0.73	0.03	0.27
Proportion surviving to adulthood	0.50	0.38	0	0.07
Mean time to adulthood (days)	12.4 (0.98)	22.4 (0.49)	—	25
Mean duration as mature pre-reproductive (days)	1.82 (0.12)	3.167 (1.45)	—	2
Mean adult life time (days)	15.3 (2.95)	10.4 (2.125)	—	12
Total number offspring	226	37	0	7
Mean number nymphs per adult	15.06 (4.89)	3.7 (2.09)	—	3.5

There were also substantial differences in performance between generations. Second-generation nymphs did slightly better on mature foliage than first generation ones, however, the opposite was true on young foliage. Two of the three measures of performance tested showed significant differences between generations on young foliage, these were fecundity (Kruskalls-Wallis statistic = 14.52,  $P < 0.001$ ) and development time ( $T = 8.26$ ,  $DF = 23$ ,  $P < 0.001$ ). However, there were no statistically significant differences in survival to maturity (two by two contingency table, Yates' corrected  $\chi^2 = 0.77$ ,  $P > 0.05$ ).

#### DISCUSSION

The effect of food quality on the population dynamics of this aphid is dramatic. The increasing leaf toughness probably renders the leaf cuticle more difficult to penetrate, and the reduced levels of soluble nitrogen in the underlying tissues, which is important for protein production, slows aphid growth and reproduction. Individuals hatching later in the year, when most leaves are mature, are faced with an increasingly difficult task of accessing ever diminishing resources, and consequently have very little chance of attaining maturity. It is easy to see how selection acts to maintain hatching in the early spring.

Although adult *Euceraphis* are large and may be able to feed on mature leaves and twigs (Gange, 1989; Stroyan, 1977), the ability of first-generation nymphs to feed on mature leaves appears to be limited. However, nymphs of later generations must feed successfully on mature leaves in order to allow the species to survive until the autumn. It is not clear how these later hatching nymphs overcome the difficulties of feeding on nutritionally poor substrates. There may be some physiological or morphological variation between generations, for example, in stylet length. The aggregation of

*Euceraphis* in midsummer onto leaves of better quality (Wratten, 1974), combined with the natural variation in leaf and tree quality will certainly serve to reduce some of the difficulties.

The slightly greater success of second-generation aphids in feeding on mature leaves, suggests that some adaptive mechanism may indeed be in place, hence allowing nymphs of later generations to feed successfully. If such an adaptation existed, it could well be traded off against increased fecundity in the first generation.

Ovariole number is known to vary between aphid generations. In *Euceraphis* the first generation possess ten ovarioles, and subsequent generations eight (Leather *et al.*, 1988). This alone will lead to differences in fecundity between generations. However, the difference in fecundity between first- and second-generation nymphs on young leaves seems too great to be explained totally by differences in ovariole numbers. The observed differences are probably due to a combination of reduced ovariole number, and the fact that second-generation aphids fed on a poorer diet than those in the first generation. Dixon (1976) reports that nymphs of the sycamore aphid (*Drepanosiphum platanoidis* Schr.) feeding on newly burst buds were heavier and more fecund than those feeding on foliage which had burst their buds only 7 days earlier. This serves to demonstrate the importance of small changes in food quality to aphid populations.

#### REFERENCES

- Ayres, M. P. & Maclean, S. F. 1987. Development of birch leaves and the growth energetics of *Epirrita autumnata* (Geometridae). *Ecology* 68: 558–568.
- Blackman, R. L. 1977. The existence of two species of *Euceraphis* (Homoptera: Aphididae) on birch in Western Europe, and a key to European and North American species of the genus. *Syst. Ent.* 2: 1–8.
- Dixon, A. F. G. 1963. Reproductive activity of the sycamore aphid, *Drepanosiphum platanoidis* (Schr.) (Hemiptera: Aphididae). *J. Animal Ecol.* 32: 33–48.
- Dixon, A. F. G. 1966. The effect of population density and nutritive status of the host on the summer reproductive activity of the sycamore aphid *Drepanosiphum platanoidis* (Schr.). *J. Animal Ecol.* 35: 105–112.
- Dixon, A. F. G. 1969. Quality and availability of food for a sycamore aphid population. In: *Animal populations in relation to their food resources*. Ed. A. Watson, Symposium No. 10. British Ecological Society, pp. 271–287, Blackwell Scientific Publications, Oxford.
- Dixon, A. F. G. 1971. The role of intra-specific mechanisms and predation in regulating the numbers of the lime aphid, *Eucallipterus tiliæ* (L.). *Oecologia Berl* 8: 179–193.
- Dixon, A. F. G. 1976. Timing of egg hatch and viability of the sycamore aphid, *Drepanosiphum platanoidis* (Schr.), at bud burst of sycamore, *Acer pseudoplatanus* L. *J. Animal Ecol.* 45: 593–603.
- van Emden, H. F. & Bashford, M. 1969. A comparison of the reproduction of *Brevicoryne brassicae* and *Myzus persicae* in relation to soluble nitrogen concentration and leaf age (leaf position) in the Brussels sprout plant. *Entomologia, Experimentalis et Applicata* 12: 351–364.
- Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565–581.
- Gange, A. C. G. 1985 Overwintering in the birch aphid, *Euceraphis punctipennis*. *Br. J. Ent. Nat. Hist.* 2: 181–183.
- Leather, S. R., *et al.* 1988. Variation in ovariole number within the Aphidoidea. *J. Nat. Hist.* 22: 381–393.
- Mittler, T. 1958. Studies on the feeding and nutrition of *Tuberolachnus salignus* Gmelin (Homoptera: Aphididae). II. The nitrogen and sugar composition of ingested phloem sap and exuded honeydew. *J. Exp. Biol.* 35: 74–84.
- Stroyan, H. L. G. 1977. *Homoptera Aphidoidea Chaitophoridae and Callaphididae*. *Handbk Ident. Insects* 2 (4a). London, Royal Entomological Society.
- Wratten, S. D. 1974. Aggregation in the birch aphid *Euceraphis punctipennis* (Zett) in relation to food quality. *J. Animal Ecol.* 43: 191–198.